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MATING BEHAVIOR AND ACTIVITY-REST PERIODICITY IN *PROTOCLYTHIA CALIFORNICA* (DIPTERA: PLATYPEZIDAE)[1]

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Introduction

The first direct observation dealing with the mating behavior of flat-footed flies was made by Snow (1894). This involved a single mating pair of the species *Calotarsa calceata* (Snow). The flies were captured with a lucky stroke of the net as they passed within an inch or two of the observer's eye and therefore too close to be brought into focus. They did not remain *in copula* in the net, so Snow was unable to contribute any notes on the mating

1. Based on studies aided by National Science Foundation grant G19006.

behavior of these flies except to mention that at the time of the capture there were a dozen or so males of this same species engaged in zigzag flight overhead.

Except for occasional observations (*e.g.*, Verrall, 1901; Kessel, 1948) that males of other platypezid species engage in aerial dances, knowledge of the mating habits of flat-footed flies did not progress for another sixty-seven years. In the meantime we had observed the mating behavior of certain balloon flies, species of the genera *Empimorpha, Hilara,* and *Empis* (Kessel and Karabinos, 1947; Kessel and Kessel, 1951; Kessel, 1955 and 1959), which belong to the Empididae, a family that most certainly is closely related to Platypezidae. The males of these empidids dance in swarms similar to those of platypezids, and in the case of these balloon flies we were able to observe the female enter the swarm of males, embrace with one of them, and then settle with him on a nearby shrub until the mating activities were completed. The observation of platypezid and empidid males dancing in similar swarms led to the supposition that the females of flat-footed flies, like those of balloon flies, enter the swarms of males to find their mates. But no evidence of such behavior was forthcoming until recently when we were able to observe the mating activities of *Platypezina pacifica* Kessel.

Mating Behavior of Protoclythias

Our observations on *Platypezina pacifica* had barely been published (Kessel and Kessel, 1961) when we discovered flies of another platypezid genus engaged in mating activities. These belonged to the species *Protoclythia californica* Kessel, and our observations were made at Steckel Park, Ventura County, California.

We arrived at Steckel Park early on the afternoon of December 19, 1961. The first hour of searching yielded no platypezids, but at 1:55 o'clock we came upon a mating pair of the species mentioned. They were resting on a horizontal leaf of a *Solanum* plant which was growing in a protected area near the river and in a spot surrounded by willow trees and bushes.

As on the occasion of our discovery of the mating pairs of *Platypezina pacifica,* we were startled by so rare a sight. Again our first reaction was to look up for the expected swarm of dancing males, and again there they were directly overhead. The general picture was the same, even to the chimney-like opening in the trees where the males engaged in their erratic zigzag flight. Once more we found the mating flies sitting with their heads directed away from each other, the larger male with his wings extended over those of the female. As before, the flies remained very quiet until they were disturbed, and then only the female responded, moving forward and towing the male behind her. When the insects were taken in the net they remained attached and continued in this union until they were transferred to the cyanide jar. They are mounted on the same pin, but on separate points, and are deposited in the collection of the California Academy of Sciences.

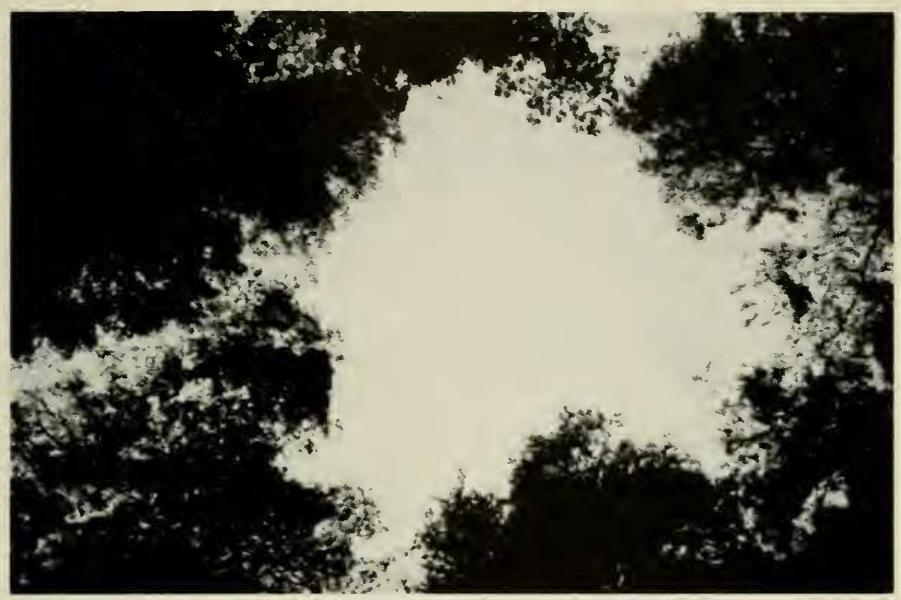

Figure 1. The mating "chimney" of *Platypezina pacifica*, surrounded by coast redwoods.

Figure 2. The mating "chimney" of *Protoclythia californica* surrounded by willows.

Although the general mating pictures for *Platypezina pacifica* and *Protoclythia californica* proved to be basically similar, we observed obvious differences pertaining to the trees outlining the "chimney," that vertically open shaft in which the males danced (figs. 1 and 2).[2] In the case of *Platypezina pacifica* the trees were coast redwoods (*Sequoia sempervirens*) while for *Protoclythia californica* they were willows (*Salix* sp.). A second difference involved the height of the trees, the redwoods of the *Platypezina* "chimney" being more than 200 feet tall, while the willows which lined the swarming opening of the protoclythias were only 20 to 25 feet high. It is of interest to note in this connection that we have always found platypezinas associated with areas where coniferous trees are growing, while we have collected many specimens of *Protoclythia californica* far removed from such forests.

Data are given in table 1 for the Steckel Park collection spot at the time (1:55 P.M.) the mating flies were taken. These include altitude of the sun, temperature, relative humidity, light intensity, barometric pressure, and wind velocity.

In order to make certain that the flies which were dancing in the "chimney" actually were males of *Protoclythia californica*, a net was passed through the swarm. The three specimens that were taken by this stroke were all males of this species. No attempts were made to capture more of the insects at that time and the remainder of the afternoon was spent in observing their actions.

Unlike the swarm observed by Snow (1894) for *Calotarsa calceata* and those which we have seen for *Calotarsa insignis* Aldrich and *Platypezina pacifica* (Kessel and Kessel, 1961), all of which were at a height of fifteen feet or more, the aggregation of dancing males in the case of *Protoclythia californica* was much lower, the altitude of flight frequently being as low as five feet. This made it possible to observe the behavior of individual insects in the swarm in more detail than had ever been possible in other species.

Reference has been made to the parallels which we have observed between the epigamic behavior of balloon flies and that which we have seen exhibited in platypezids. In our publications dealing with balloon flies we have more than once made the statement that we have observed the female enter a swarm of males, embrace one of them, and then settle with him on a nearby shrub. Also, in our last paper (Kessel and Kessel, 1961) we recorded our observation of a mating pair of *Platypezina pacifica* descending from the swarm of males and added the comment: "It is evident that the female, like those of balloon flies, had selected her mate from the dancing swarm, and the pair were descending to the groundcover plants to complete their nuptial activities." In these instances we have attributed the initiative in selecting a mate to the female, but from our closer observation of swarming proto-

2. We wish to thank Mr. Maurice Giles for preparing the three black-and-white prints from our kodachromes for use as illustrations in this paper.

Table 1

Generalized data for various times of the day at the "chimney" location in Steckel Park, Ventura County, California, on December 19 and 20, 1961. Pacific Standard Time is given to the nearest 5 minutes and no correction is made for the east-of-meridian location. Temperature is given to the nearest degree Fahrenheit and relative humidity to the nearest per cent. Light intensity with the meter directed up the "chimney" is recorded to the nearest 50 foot-candles and with it pointed toward the ground under the "chimney" the light intensity is given to the nearest 5 foot-candles. The barometric pressure on both days was 29.6 inches and the wind velocity was never higher than 5 miles per hour.

Time P.S.T.	Altitude of sun	Temperature	Relative humidity	Light up "chimney"	Light down "chimney"
9:05 A.M.	20°10′	60°	78%	300	20
9:15	21°43′	63°	75%	300	25
9:40	25°15′	64°	74%	400	30
10:30	29°40′	64°	72%	500	30
11:00	31°20′	64°	67%	500	30
11:20	32°18′	64°	67%	500	30
12:00 M.	33°07′	64°	64%	450	30
12:55 P.M.	31°15′	66°	64%	400	30
1:05	30°35′	66°	64%	300	25
1:15	29°55′	65°	65%	300	25
1:30	28°50′	65°	67%	300	25
1:55	26°48′	64°	68%	300	20
2:55	19°40′	64°	72%	300	20
3:10	17°45′	64°	76%	250	10

clythias we are now convinced that the male is not passive in the mate-selecting process.

It is evident that in both balloon flies and platypezids mating takes place only in the swarms where the males are waiting for the females to come to them. We have often observed males and females belonging to the same species sitting in close proximity on the same leaf but in only one case did the sexes not ignore one another under such circumstances. The exception occurred when we were collecting in the Botanical Gardens of the University of California at Los Angeles and involved *Clythia* (=*Platypeza*) *agarici* (Willard). A male that was sitting close to a female suddenly jumped on her back but she promptly threw him off. It appears that the female must be stimulated by the recognition of her own special species' pattern of epigamic behavior before she will accept a mate, and that she encounters this pattern only in the swarm of dancing males. She doubtless recognizes them as belonging to her own species by some such specific symbol as the flashes of their balloons (*Empis, Empimorpha, Hilara*), the scintillations of the flags on their feet (*Calotarsa insignis*), or other decorations and characteristics of their extended posterior tarsi (*Calotarsa calceata, Platypezina pacifica, Protoclythia californica*). Once she has recognized the swarm as consisting of males of her species she flies in among them. On a leaf she may not recognize a potential mate, at least she repulses any advances that he may make, but in the proper swarm she is receptive and perhaps even eager. In the case of the balloon fly *Empimorpha geneatis* Melander we saw the female enter the swarm of males and there embrace with one of them. We presumed at the time that she had taken the initiative and selected a mate, but the joining of the flies happened so quickly once she had entered the swarm that it was impossible to be sure which sex had made the advances.

Because of the lower swarming flight of *Protoclythia californica* we were near enough to the insects to ascertain that all of the dancing flies were males. It was also easily seen that with even the slightest indication of a breeze they would all face into it, "standing" still in the air or rising and falling with only slow progress forward. When a male had finally reached the periphery of the "chimney" area, he would swing back more or less to the opposite margin of the swarm and once more face into the breeze. When there was no evident air movement, the flies would usually merely turn about and progress slowly through the swarm to the opposite side of the "chimney." It was not possible for us to determine if there was a slight updraft of warmer air in the vertically open shaft. There is opportunity to speculate on the possible relationship between air movements or temperature gradients and the selection of these "chimneys" for nuptial flights.

In watching the swarm of protoclythias we noticed that when a male came closer than about four inches to another fly, the two insects would invariably dart toward each other, only to veer away before contact was made. It seemed as though the males were inspecting one another, each to determine if the other fly was a female. The males were very alert in these actions and any female entering the swarm would have been grabbed by the first male she approached in her line of flight.

The compound eyes of male platypezids are both larger and more complex than those of the female. They are so large, in fact, that they are contiguous along the midline in front. As for the complexity of the eyes themselves, each is divided by a shallow groove into an upper portion possessing larger facets and a lower part having smaller facets. By contrast, the female has her compound eyes widely separated and all of her facets are of uniform size, about equivalent to those of the lower area of the male's eye. There has been considerable speculation as to the significance of these differences. Presumably the more complex eyes of the male give him wider and sharper vision than the female enjoys. It seemed illogical, therefore, to suppose that this more elaborate optical equipment is without significance in the mating behavior of these flies which would certainly be the case if the male did nothing but dance with his fellows and wait passively for a female to select him. We now know that in the swarm the male darts aggressively at every fly that comes within range. The first male to recognize the female and to get to her will take her as his mate.

We have presumed that the events leading up to pairing are similar in the balloon flies and the platypezids, and this in spite of the different copulation positions which the members of their respective families, Empididae and Platypezidae, typically assume. In the cases of the balloon flies which we have observed the male sits astride the female with his head in the same direction as hers, whereas in the platypezids the male and the female are directed away from each other and with only the tips of their abdomens in contact. These positions seem to be correlated with the nature of the male genitalia which in empidids are characteristically directed upward and forward and in typical platypezids are pointed downward and forward. These would seem to be major distinctions until one considers the fact that the male platypezid, as he approaches the completion of metamorphosis, has genitalia positioned like those of empidids. Only later, but while the fly is still in the puparium, do the genitalia begin to rotate to assume their final direction. By the time of emergence, the rotation is nearing completion of a 180° movement, and by the time the male is sexually mature the hypopygium is directed downward as well as forward. It is likely that this difference achieved by the 180° rotation of the genitalia in platypezids requires divergent copulatory positions in the two families. But in no way do the different positions and structures here described indicate that the two families are not closely related as we have believed.

Returning to the consideration of the swarm of *Protoclythia californica* which we observed at Steckel Park, some of the dancing males continued their activities as late as 3:10 P.M. when the sun disappeared behind the hills (see table 1 for data). However, their numbers had been gradually diminishing before that time. Almost as the sun vanished, the last males disappeared from the "chimney." No platypezids had been seen on the bushes since 2:55 o'clock.

Early next morning we returned to the swarming site to ascertain when and under what conditions the males would resume their dancing, but in spite of the fact that the day was clear and sunny like the one before, no flies appeared in the "chimney" until early afternoon. Nevertheless, at 9:05 A.M. (see table 1 for data) we did begin to see protoclythias of both sexes moving about on the leaves of bushes under the "chimney" area, stopping here and there to feed. For approximately the next two hours the flies continued their morning exercise and feeding period. Then came the rest period, beginning as abruptly as had the morning activity period which it replaced.

Activity-rest Periodicity

Our many years of platypezid collecting during all of the seasons, from Alaska to Mexico and from the Atlantic to the Pacific, had led us to conclude that the more sun-loving flat-footed flies interrupt their daily activities to take a siesta during the middle of the day. So definite was this feeling that we often found ourselves planning our collecting stops so as to avoid the hour or so before and after noon. When we made a point of looking into the matter we found that our impression agreed with the facts. While those species of Platypezidae which frequent environments of deep shade do not engage in well defined rest periods, all of those forms which are to be found typically in habitats of filtered sunshine seem to resort to a mid-day period of inactivity. Representative of the shade-dwelling forms are *Platypezina pacifica*, *Platypezina diversa* (Johnson), *Calotarsa insignis*, *Agathomyia lucifuga* Kessel, *Agathomyia nemophila* Kessel, and *Agathomyia sylvania* Kessel. Examples of the sun-loving species are *Protoclythia californica*, *Clythia agarici* (Willard), *Clythia polypori* (Willard), *Clythia dymka* Kessel, *Clythia cinerea* (Snow), *Clythia hunteri* Kessel, and *Clythia coraxa* Kessel. The species of *Metaclythia* would doubtless fall into this second category. Our experience indicates that the species of *Callomyia* are intermediate in their sun-shade inclinations.

Reference has been made to our observation that protoclythias indulge in a morning activity period during which they feed and run about on the leaves. It has also been our observation that all of the sun-loving species have such a time of activity and that they exhibit a corresponding period in the afternoon. Their mid-day rest occupies the time between these two. Everywhere we have been impressed by the rather sudden onset and abrupt termination of these periods. We were also impressed by the fact that the activity periods of *C. cinerea* in Alaska are longer than those exhibited by this species in the San Francisco Bay area of California. Similarly, for *C. coraxa* the activity periods are longer in the San Francisco region than are those which we found for this species in San Diego County, California, some 375 miles to the south. These longer activity periods would seem to be related in some way to the longer days one encounters in our hemisphere as he travels north during the time between the vernal and autumnal equinoxes.

We presumed that such physical factors of the environment as temperature, relative humidity, and light intensity were the stimuli which regulated the activity and rest periods of these flies, but having provided ourselves with thermometer, hygrometer, and light meter we were quickly convinced that the data recorded by these instruments did not reveal the whole story. Too often there had been no changes or only minor ones in the factors just mentioned when there would be a sudden termination to the mid-day rest period. For instance, where at most only an occasional platypezid had been seen during the previous two hours or so, we were suddenly confronted with the problem of which fly to catch.

Considering this matter, we began to think about the discoveries which have been made in recent years in connection with the circadian phenomena of insects and other organisms (von Frisch, 1950; von Frisch and Lindauer, 1954; Lindauer, 1954, 1960; Lees, 1960; Pittendrigh, 1954, 1960; Bruce and Pittendrigh, 1957; Harker, 1960; Birukow, 1960; Breamer, 1960; and Renner, 1957, 1958, 1959, 1960).[3] Could it be that we were dealing with a biological time clock, some internal mechanism which functions with a twenty-four hour periodicity and prompts our flies to become active or inactive, depending upon the rhythm of their particular species? If such an endogenous mechanism does exist, does it act alone, or is it correlated with and triggered by certain periodically recurring exogenous factors?

Renner (1958, 1959) has shown that the time-sense of honeybees is based, under normal circumstances, on both endogenous and exogenous elements. He was able to show that while the insects were able to orient themselves in time by means of an endogenous mechanism alone under laboratory conditions, they used both internal and external factors when they were in their natural surroundings. It seemed reasonable, therefore, to suspect that our flies, which like the bees are among the highest of insects, may possess a somewhat similar internal clock, a mechanism which is synchronized with one or more recurrent environmental factors.

Aschoff (1960) has applied the term "Zeitgeber" to the sum-total of the recurring components of the environment which serve to synchronize an organism's circadian rhythm with its surroundings. Adapting this word to our English terminology, it should be pointed out that the zeitgeber must be periodically operative. An exogenous timer of this type might include alternating factors such as light and darkness, continuously changing factors such as the daily course of temperature, or even short signals which occur only once or twice in a twenty-four hour period. However simple or complex the zeitgeber may be, its function is to determine phase, to synchronize any multiplicity of circadian clocks that may be present within an organism, and to synchronize and keep in phase all of the individuals of the species which are in the environment under consideration. As Aschoff has also pointed out, this last function of the zeitgeber implies that all of the individuals of the species have the same sensitivity to the timer, because if this were not the case the organisms would not be in phase and one would not find what we call a species' pattern.

We may suppose that the rest and activity periods of platypezids indicate a circadian periodicity which is triggered by a zeitgeber but, as we have already suggested, the exogenous timer in this case must involve an environmental component other than temperature, relative humidity, and light intensity. Some or all of these may contribute to the zeitgeber, but we are convinced that some other factor must be the recognizable exogenous element.

In considering what the missing component might be, we thought about

3. We are indebted to Dr. William J. Hamilton of the California Academy of Sciences for referring us to some of this literature and also for lending us certain reprints from his personal files.

our observation that those species of platypezids which inhabit deep woods lack a mid-day rest period. We also recalled the longer activity periods of sun-loving platypezids as one travels northward to Alaska during the longer days of summer. We wondered, therefore, if the altitude of the sun could be the critical element of the zeitgeber which had been missing from our data. Perhaps the time-sense of our flies which lets them know when to begin and when to terminate their morning and afternoon activity periods is dependent upon a circadian periodicity which is triggered by a "built-in" sextant. In order to test this hypothesis of a sun-oriented rhythm we decided to add a sextant to our equipment. Dr. G Dallas Hanna of the California Academy of Sciences advised us to use a bubble sextant inasmuch as we would usually be working where it would be impossible to observe the horizon. We are indebted to Dr. Hanna for the loan of such an instrument, the one we have been using to obtain our sun-altitude readings.

The rest period for *Protoclythia californica* at Steckel Park on December 20, 1961, began at approximately 11:00 A.M. At that time a male alighted on the *Solanum* plant under the "chimney" where the copulating pair had been captured the day before. He walked about for a second or two and then settled down near the edge of the leaf with his head directed toward its tip (fig. 3). This was a characteristic stance and position on the leaf for a platypezid during the mid-day rest period as we had observed it in several

Figure 3. The observed male of *Protoclythia californica* may be located sitting along the margin of the large leaf where he was difficult to see and maintained his position for the entire mid-day rest period.

species of *Clythia*. These insects always seem to rest at or very near the edge of the leaf and with the head pointed toward its tip. Often they take up a position at the very tip of the leaf. The protective value of these marginal sites is evident when one considers the hazards to which the leaf margin is subject and the leaf scars which result therefrom. The fact that the fly sits with his body parallel to the leaf veins also adds to his protection. While at such times the insects show no interest in feeding and are not easily disturbed, collecting them during this rest period is not ordinarily profitable because they are so easily overlooked.

It was evident almost immediately that the male before us had settled down for his mid-day rest. At noon he had shown absolutely no movement and no other platypezids had been observed. This inactivity continued until 12:55 P.M. when the first signs that the rest period was ending became evident. While the male under observation still sat undisturbed, two other males were noticed walking about on other plants in the area. A third male was observed dancing alone in the "chimney." Data for the several times mentioned in this account are given in table 1.

At 1:05 P.M. the male under special observation shifted himself and walked around to the opposite side of the leaf, this time taking up a position with his head directed toward the petiole. Shortly thereafter he flew away but we were unable to observe whether or not he entered the "chimney." By this time there were several flies dancing there and by 1:15 o'clock their number had increased to more than a dozen.

Our observations at Steckel Park indicate therefore that the mid-day rest period for *Protoclythia californica* on December 20, 1961, began at approximately 11:00 A.M. and terminated shortly after 1:00 P.M. Because of the symmetrical shape of the sun's altitude curve, each altitude achieved during the day, except that of noon, occurs twice that day, once in the morning and once in the afternoon. Therefore, the altitude of the sun at 11:00 A.M. and at 1:00 P.M. would be the same on any one day, providing one is dealing with solar time. Our data given in table 1 are only approximate as noted in the explanation. These generalized data, plus the fact that for the most part we are dealing with a single set of observations made in one place under one set of conditions, justify only generalized conclusions. We present these here in the nature of a preliminary report.

The sextant reading taken at 11:00 o'clock when the male under special observation began his siesta was 31°20′. At the time he flew away, the sun had declined to an altitude of 30°35′. Because the male in question did not "wake up" until after some of the other protoclythias in the vicinity had become active, we must conclude that not all of a species' individuals in an area begin and end their rest period at the same instant. It may seem to the collector in the field that they do, but it is evident that we must allow a little individual variation even in response to a biological clock such as we are dealing with here. Allowing this at the beginning and again at the end of the rest period, we approximate the angle of 30 degrees as the altitude of the sun which indicates the onset and the termination of the siesta time, as well as the conclusion of the morning and the beginning of the afternoon activity periods.

It has been stated that the first protoclythias observed in the morning appeared at 9:05 o'clock at which time the angle of the sun was 20°10′. It has also been noted that the last flies seen in the afternoon disappeared at 3:10 o'clock when the angle of the sun was 17°45′. Until then some of the males had been dancing in the "chimney" although their numbers had been diminishing for some minutes. The last flies to be seen walking or running about on the leaves had been observed 15 minutes earlier. Because no swarming of the males occurred during the morning and this phenomenon has been shown to be a part of the mating behavior, we may regard it as something special which is not entirely regulated by the same factors which control the regular activity periods. While it is true that some of the males remained in the swarm until the sun disappeared behind the hills, the last flies seen walking about and feeding on the leaves had been observed at 2:55 P.M. when the angle of the sun's altitude was 19°40′. This figure agrees well with the 20°10′ of the sextant reading when the insects began their activity-feeding period in the morning. Our data, therefore, lead us to the generalization that the times of activity for *Protoclythia californica* occupy the periods when the altitude of the sun is between the angles of 20 and 30 degrees.

Owing to the lower maximum altitude of the sun and its less abrupt ascendancy and descendancy during the longer summer days in more northern latitudes, there is a longer period each morning and afternoon in such regions during which the angle of the sun is between 20 and 30 degrees. On this basis one would expect that the activity periods of the sun-loving species of platypezids would be correspondingly extended so as to both begin earlier and last later. This result would be in accord with our observations that the activity periods of *Clythia cinerea* in Alaska are longer than those of the same species in California at the same time of the summer. This extension of the activity periods obviously reduces the length of the rest periods. In fact we may suppose that for those platypezids which respond to the same sun angles in the same ways as do protoclythias, the mid-day rest period would not only be abbreviated in Alaska, but actually eliminated wherever the altitude of the sun does not pass above the 30-degree mark.

Examination of table 1 does not suggest that the temperature factor is directly involved with the onset and termination of the activity periods. The same may be said for the data given in the two light-intensity columns. On the other hand the figures on relative humidity reveal that there was an abrupt 5 per cent drop in the value of this factor between 10:30 and 11:00 A.M., just prior to the beginning of the mid-day rest period. However, the data show no immediate return at the conclusion of the rest period to the higher relative-humidity reading of 72 per cent obtained at 10:30 o'clock. This figure was reached by 2:55 P.M. but that was when the afternoon activity period was ending, not beginning. We may conclude, therefore, that the data support our general field impressions. Relative humidity, like temperature and light intensity, seems to play no direct role in the regulation of the activity and rest periods of platypezids. Possibly, acting together with temperature and barometric pressure to determine the saturation deficit, it may participate in the zeitgeber. There is little doubt, however, that the data here reported point to the angle of the sun's altitude as the time signal or chief exogenous regulator of the circadian activity-rest periodicity in platypezids.

Granting that these flies do possess such a circadian periodicity, one may well ask what the value of it could be to the species. By its very nature, such a rhythm involves innate factors, so we must conclude that it is a physiological phenomenon with a genetic basis. The species' pattern of restricted feeding-activity periods, with rest intervals between them, is likely to possess a survival value. In considering what this advantage to the species might be, it is logical to determine first what are the chief natural enemies of the flies. There seems to be no doubt that there are birds, those species which frequent the marginal woods which also constitute the filtered-sun habitats of the platypezids here being considered. If the birds, too, have periods of greater and less activity, then it is advantageous to the flies to avoid those intervals when the birds are more active. When platypezids are running about, they are among the most obvious of insects considering their small-to-medium size. So unique is their manner of movement, running to and fro in a series of darts and stops, that it is often easy to spot one of them from a distance of many feet. While this attention-attracting behavior constitutes a welcome advantage to the entomologist who is searching for these relatively rare insects, it would seem to constitute a real disadvantage to the flies in the matter of their bird predators. But this disadvantage would be overcome, in part at least, if the flies would alternate activity periods with the insectivorous and omnivorous birds which occupy the same habitat.

On our extensive collecting trips, during which we camped out most of the time, we have gained the impression that in general birds are early risers and, after the night's fast, spend the first several hours of the morning in search of food. When there is an abundance of food, many of the birds cease their hunting in the middle of the morning and retire for a rest period. Contrasting platypezids with birds, we have seen that these flies are late risers and do not make their appearance in numbers until the middle of the morning, or about the time that the number of feeding birds is noticeably diminished. It is apparent, therefore, that while the flies are feeding, many of the birds are likely to be resting. Late in the morning and continuing until the early afternoon comes the platypezids' mid-day rest period during which time there may be another surge of active birds. Once again, in the early afternoon, fewer birds are in evidence and the flies come out for an activity period. General feeding time for the birds comes once more in the late afternoon, but by this time the platypezids have disappeared for the day.

In order to see if there might be some credibility to this hypothesis, we decided to keep a record of the birds which visited the feeding station at our home in Novato, California, on a particular day which happened to be February 17, 1962. The feeding platform is located in ideal platypezid territory along the margin of virgin woods where we have often observed flat-footed flies of several species. The trees making up the woods are mostly oaks and California laurels, and underneath them is an understory of low bushes. All birds visible in the immediate area at the time of a count were included, regardless of whether they were on the platform, or on the ground, or in the bushes. For the period between 8:00 and 10:00 A.M. and after 3:00 P.M., the counts were made every 15 minutes. From 10:00 A.M. to 3:00 P.M. they were made every 5 minutes.

The results of the count (table 2) fit in well with the hypothesis which we have proposed. The expected morning surge was very evident with its average of 17.4 birds per count. Then as the morning activity period for the flies began at 9:00 o'clock, the number of birds dropped off abruptly. For the entire fly-activity period ending at 11:00 A.M. the birds figures remained rather low with an average of 2.44 per count. During the mid-day rest period for the flies, from 11:00 until 1:00 o'clock, there was a substantial increase of some 50 per cent in the average number of feeding birds present to give a figure of 3.74 per count. Between 11:30 and 11:55 there was a noticeable rise in the counts, with a maximum number of 12 birds representing 4 species (junco, brown towhee, titmouse, and chickadee). These figures indicate that it would be worthwhile for the platypezids to abstain from engaging in their attention-attracting movements during this period of greater activity for the birds. For the afternoon activity periods of the flies, from 1:00 to 3:00 o'clock, the average number of birds per count dropped to 2.56. During this interval the birds which we saw appeared to be more lethargic and one even seemed to be asleep on the feeding platform for several minutes. After 3:00 o'clock, when the second fly-activity period of the day was ended, there was no evident increase in bird numbers until about 4:15 P.M. At 4:45 o'clock when the last count was made, there had been an increase to 10, perhaps representing the beginning of the expected surge in numbers of the evening feeding period of the birds. Although the average number of birds per count had increased to 3.12 between 3:00 and 4:45, this increase was so slow in coming that as far as danger from birds is concerned these figures give little reason for the flies to go into hiding as early as 3:00 P.M. Of course, if the activity periods of these insects are determined on the lower

Table 2

Number of birds observed at different times of the day at a feeding station located at Novato, California, and recorded on February 17, 1962, together with the average number of birds per count for the several periods which are indicated.

P.S.T.	Number	Period and average	P.S.T.	Number	Period and average
8:00 A.M.	12		12:35	3	
8:15	15	Morning bird-	12:40	2	Mid-day rest
8:30	22	activity	12:45	4	period for
8:45	18	period.	12:50	4	flies (cont.)
9:00	20	Average 17.4	12:55	4	
……	……	……	……	……	……
9:15	4		1:00	0	
9:30	3		1:05	3	
9:45	1		1:10	6	
10:00	7	Morning fly-	1:15	3	
10:05	0	activity	1:20	1	
10:10	2	period.	1:25	2	
10:15	4	Average 2.44.	1:30	4	
10:20	2	Decrease in	1:35	2	
10:25	5	bird activities.	1:40	2	Afternoon fly-
10:30	2		1:45	2	activity
10:35	3		1:50	2	period.
10:40	2		1:55	3	Average 2.56.
10:45	1		2:00	3	Decrease in
10:50	1		2:05	3	bird activities.
10:55	2		2:10	2	
11:00	0		2·15	3	
……	……	……	2:20	2	
11:05	5		2:25	3	
11:10	4		2:30	3	
11:15	1		2:35	2	
11:20	1		2:40	1	
11:25	0	Mid-day rest	2:45	5	
11:30	4	period for	2:50	3	
11:35	12	flies.	2:55	3	
11:40	8	Average 3.74.	3:00	1	
11:45	4	Increase in	……	……	……
11:50	6	bird activities.	3:15	1	
11:55	6		3:30	2	
12:00 M	2		3:45	0	Evening bird-
12:05 P.M.	2		4:00	2	activity
12:10	0		4:15	5	period.
12:15	4		4:30	4	Average 3.12.
12:20	2		4:45	10	
12:25	5		……	……	……
12:30	3				

level by a particular angle of the sun's altitude as we have postulated, then this could not be decreased for the afternoon period without likewise decreasing it for the morning period. And this would put the flies into greater jeopardy by forcing their early activities into conflict with the morning surge of feeding birds.

It is recognized, of course, that to be wholly significant the counts of birds observed feeding at different times during the day should have been made in the same place and same time of year as the fly study with which they are compared, not 300 miles or so more to the north and 2 months later as they were. But because it was impossible to make the counts at Steckel Park on December 20, these less-desirable data from Novato and recorded on February 17 are substituted.

Our comments concerning the attention-attracting movements of platypezid flies as they run about on leaves in their unique jerky tempo, deserve additional comment. One cannot help but wonder why such a jeopardy-inviting activity has been maintained by these flies. Its disadvantages are so obvious when we consider the matter of bird enemies. Does this habit seemingly have any conpensating advantages?

Howlett (1921) is of the opinion that it does have such advantages. While he agrees that the unique movements of flat-footed flies are attention arresting, and therefore can hardly make these insects less conspicuous to such important enemies as birds, nevertheless he believes that they have a protective value in that they make the capture of the fly more difficult than if it were sitting still or "standing" in the air. Howlett also cites the cases of several arthropods which supposedly obtain protection by means of their obvious tetanic actions. He refers to several of these which, when disturbed, cause the body to vibrate so rapidly that the observer sees only a blurred area. He thinks that it is likely that in platypezids "the rapidly alternating translatory motion of the whole insect may be another means of achieving a similar result."

While Howlett attempts to make a convincing case of these points, our observations indicate that he is wrong in his major premise that the darting-stopping movements of platypezids are executed *only* when the flies are disturbed by the movement of some object in the vicinity. Over and over again we have cautiously approached a likely looking "platypezid bush" from behind good cover and from our vantage point observed several flies variously engaged. While at the moment some were quietly feeding, the others were moving about in their to-and-fro fashion searching for food. A few minutes later and without cause for alarm, the feeders might be running and the runners quieted down. We can hardly agree, therefore, with Howlett's contention that the movements are wholly defensive maneuvers.

Platypezids are often extremely quick in movement. This is particularly true of their departure flights, that is, when they leave the immediate vicinity, not just move to an adjacent leaf. They may have been "floating" in the air in zigzag fashion, "standing" practically motionless in the air, or running or sitting on leaves. In any case their departure is instantaneous, without any discernible preparatory movements or attitudes. It is also instantaneous in the actual departure which is so rapid that the eye can very seldom follow it. It can be truthfully said in almost every instance that "if you saw it leave it was not a platypezid." Most frequently the fly leaves completely, that is, it does not just fly a few feet or yards and then settle down or return.

Very few, if any, of the dipterans that we have encountered have this habit of complete and rapid departure, or at least utilize it at all frequently. In the platypezids it is used on many occasions: when they are disturbed by a sudden breeze, another insect, a bird, or a falling twig or leaf, sometimes even by abrupt exposure to bright sun or heavy shadow. It is also used when a person causes a disturbance by close approach, considerable movement, or shaking the foliage. Significantly, however, the same method is followed when the most critical observation can discern no disturbing condition; this is just the usual manner in which platypezids depart from any particular spot.

A point of special interest in connection with the departure flight is the fact that it can take place in the midst of any of the fly's normal activities. As already mentioned, flies leave from a place in the air or from a leaf. Furthermore, when from a leaf this flight may occur in an entirely typical manner whether the fly has been busily feeding at one spot, running rapidly over a leaf, or remaining very quiet during a rest period. In any of these cases the fly is there and the next instant it is not. It should be pointed out, however, that quite logically these flies spontaneously take flight less often and are disturbed least by external factors when they are quietly feeding or in a rest period, or when it is relatively dark and cold. Departure flights are more frequent and most easily caused by disturbance when the flies are running on leaves, or "standing" in the air, or when the light intensity and temperature are high.

In considering the subject of external disturbance of platypezid activity, aside from the relation of actual departure flights, it can be said that any one of many nonextreme factors may bring about a change of activity. This is most easily seen when a fly is busy feeding in one spot and, when disturbed only slightly, begins to run in typical jerky fashion over the leaf. It should be remembered in this connection that the fly's feeding activity on the leaf consists normally of two phases, one of more or less rapid running and at the same time testing for the presence of food and the momentary stopping to actually take food when it is found in tiny amounts, the other phase involving feeding at one spot of greater abundance. When the flies are undisturbed these two phases alternate with no regular pattern whatsoever. The two phases together make up the general pattern and shift according to the circumstances. One of the conditions which seem capable of serving as the stimulus for a temporary shift to the running phase, yet without breaking the pattern, is some slight external disturbance such as the casual yet obvious approach of a person. Howlett's observations, limited to a study of two platypezids, led him to interpret this shift to the running phase as a special defensive maneuver.

Perhaps the running behavior of flat-footed flies does have some such protective value as Howlett has suggested. Our opinion, however, is that this is of minor importance, if indeed it has any such significance. Instead, we are convinced that the advantage to the species of this display of so much haste and such an expenditure of energy is correlated with the search for food. Platypezid flies are not predaceous, so they need not run rapidly to catch prey. But they do glean their nourishment from inconspicuous accumulations on such flat surfaces as leaves, and because of the limited quantity of this food often available to them they have survived by the utilization of an innate capacity to scrounge for their food. Such scrounging becomes most efficient when the movements are rapid and to the point of discovery.

That platypezids utilize their characteristic jerky movements when they are completely undisturbed and their only motivation is the search for food was made very clear to us by the following laboratory observations. Larvae of both *Calotarsa insignis* and *Clythia agarici* had been collected in large numbers and placed in rearing cages. When it came time for the insects to emerge as adults, so many of them appeared that after we had mounted and preserved all that we could use, a hundred or more flies of each species were left over. So we decided to release them in the laboratory and to observe their behavior.

The room was a small one measuring about 7 by 14 feet. There were no windows and the only natural light was from a small skylight at one end of the ceiling. Artificial illumination was provided by two overhead fixtures and a desk lamp. Many of the flies had emerged as long as two days previously and none of them had received nourishment. When these hungry flies were released they dispersed and within a few minutes they seemed to be everywhere, on the floor, bookcase, collection case, filing cabinet, and desk. And everywhere they exhibited the same to-and-fro, stop-and-go search for something to eat. As we had expected, few of them went to the skylight; instead, most of them went to the lower levels of the room, particularly the desk and the floor. It is of interest to note that this preference for the lower levels agrees with their lower-story habitats in woods.

Although all of the flies seemed to us to ignore our presence and to be concerned only with their search for food, one might argue that the reverse was true and that in conformity with Howlett's theory they were exhibiting their incessant erratic movements because they were in artificial surroundings and very much disturbed. But this possibility was eliminated very soon when some of the flies on the desk happened upon the cleared area where we had just eaten our sandwich lunch. All of the crumbs had been brushed up and nothing of food value remained as far as we could see. But to the flies there were spots of nourishment present and they stopped to feed on them. The insects were so intent on their feeding that they were undisturbed when we placed an open-base-type binocular microscope over them and brought them into focus. By this means we were able to see them feeding in house-fly fashion on the film spots of food which they had discovered on the desk. But finishing in one spot they were always in a hurry to find another, and in so doing fell into their familiar pattern of movement.

We are therefore convinced that these peculiar motions indulged in by platypezids are not defensive measures such as to make them more difficult to capture or to scrutinize, but rather are only a part of their search-for-food pattern. If by such movements the flies also run the danger of attracting the attention of birds, that is a hazard which the species must endure. If this hazard has been reduced by the expedient of alternating feeding periods with birds, this constitutes a survival factor worth perpetuating. But the business of getting food must go on.

Summary

The mating behavior of *Protoclythia californica* here described involves only the second occasion on which mating pairs of flat-footed flies have been studied; the first observations dealing with *Platypezina pacifica* having already been reported by us. Owing to the lower height of the willow trees which outlined the swarming "chimney" of *P. californica* as compared with the very tall redwoods of the platypezina "chimney," the level of the swarm was much lower in the case of the protoclythias. This made it possible to study them at very close range and thereby gain a clearer picture of the epigamic behavior of these flies. It is evident that the mating behavior of these two species is essentially the same and presumably it is representative not only of the two genera to which they belong but also of the family Platypezidae.

The males gather in swarms to dance in a "chimney" outlined by trees. Here they wait for individual females to approach the swarm. While the females have always been observed to ignore or repulse the advances of males in other situations, they are positively erotropic once they recognize that the swarm represents their own species. The receptive female enters the swarm of males and is grabbed by the first one she approaches in her line of flight. Copulation is initiated in the swarm and union is accomplished with the heads of the flies pointing in opposite directions. The female assumes the initiative in flight, the male being towed backward as the pair descend to complete their nuptial activities on a lower-story shrub below the "chimney." The female continues to haul the male around as she walks over the leaves in search of a suitable resting place. The peculiar mating position assumed by

these flies seems to be correlated with the nature of the male genitalia which are rotated 180 degrees so as to be directed downward and forward.

Long experience in collecting flat-footed flies convinced us that the more sun-loving species which inhabit the areas along the margins of woods have well defined morning and afternoon periods of activity, with a rest period occupying the mid-day interval between them. We were impressed by the rather sudden onset and abrupt termination of these periods and also by our observation that the activity periods for a particular species are longer in the more northern latitudes.

It is our opinion that the activity-rest periodicity of these flies is regulated by a circadian rhythm which functions as a biological clock on a twenty-four hour basis. Searching for the exogenous factors which may trigger this presumed endogenous mechanism, we concluded that temperature, relative humidity, and light intensity do not qualify for this role. Only the altitude of the sun seems to be identifiable as an exogenous timing element.

Observations made at Steckel Park, Ventura County, California, on December 20, 1961, indicate that the activity times of this species coincide with the periods when the sun's altitude is between the angles of 20 and 30 degrees. On the day and at the place stated, the morning activity period lasted approximately from 9:00 to 11:00 o'clock, the rest period from 11:00 until 1:00 o'clock, and the afternoon activity period from 1:00 to 3:00 P.M.

In consideration of what value this periodicity may possess for the flies, we propose that it is advantageous for them to alternate activity periods with birds, which are their chief predators. Our general impression, gained during much field work and supported by limited data, is that birds tend to be early risers and spend the first hours of the day in search of food, after which they may retire for a rest period. Platypezids, by contrast, are late risers and do not make their appearance in numbers until the middle of the morning, so while the flies are feeding many of the birds are resting. When the flies take their mid-day siesta, there may be another increase of feeding birds. As the birds once more become less active in the afternoon, the flies appear again for an activity period. General feeding time for the birds is evident again in the late afternoon, but by this time the platypezids have retired for the day.

Platypezids characteristically attract attention by their to-and-fro stop-and-go movements as they run about on leaves. It was proposed long ago that these darting-stopping movements are executed only when the flies are disturbed and that they have the protective value of making capture more difficult. We cannot agree with this viewpoint. Instead, we hold that the jerky running of these flies is merely a phase of their feeding activity, a part of their search-for-food pattern. Adult platypezids glean their nourishment from inconspicuous accumulations on such flat surfaces as leaves and, because of the limited supply, they must often scrounge for their food. Such scrounging becomes most productive when the movements of the search are rapid and the testing stops are brief.

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